

Canopy transpiration of a *Larix sibirica* and *Pinus sylvestris* forest in Central Siberia

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ABSTRACT

Russian boreal forests represent the largest forested region on Earth and comprise one-fifth of the world's forest cover. The two most common genera in Siberia are *Larix* and *Pinus*, which together cover more than 80% of the region's forested area. One observable ongoing effect of climate warming is that natural populations of Siberian larch are gradually being replaced by Scots pine. The present work focuses on comparing effects of environmental variables on sap flow density in two even-aged stands of *Larix sibirica* and *Pinus sylvestris*. While the two study stands were identical in age (49 years) with similar basal areas and leaf area index, they exhibited very different transpiration rates and response mechanisms to environmental signals. Stand water use was higher for larch than it was for pine, even though transpiration for deciduous larch trees occurred over shorter time periods. The cumulative annual transpiration of the larch stand was 284 ± 4 mm measured over two consecutive growing seasons (2015–2016), while for pine this was 20% lower. Seasonal transpiration accounted for 50% and 40% of the reference evapotranspiration and 91% and 67% of growing season precipitation for larch and pine, respectively. Water stored in soil provided an important source of water for transpiration, observed as roughly 100 mm, which was then replenished from snowmelt the following spring. The greatest difference between two species related to how well they controlled transpiration, notably in the context of high vapor pressure deficit; under these conditions, pine maintained greater control over transpiration than larch. For all soil moisture levels measured, larch transpired more water than pine. Importantly, our results point to potential future effects of global warming, most notably an increasing decline of larch forests, changes in the ratio between latent and sensitive heat fluxes, and significant modifications in ecosystem water availability.

1. Introduction

Transpiration dynamics of boreal forests have changed as a result of climate warming and subsequent changes in tree species composition (Bonan, 2008). The boreal forest (also known as the taiga) is world's largest terrestrial biome, making up one-third of the world's total forest cover, the largest areas of which (60%) are located in Russia (FAO, 2016). This region of boreal forests serves an important role in the

global water cycle, providing 9.5% of terrestrial evapotranspiration (Schlesinger and Jasechko, 2014). The most important conifers in the boreal forests belong to genera *Pinus*, *Picea*, and *Larix*. While *Picea* and *Pinus* are widely distributed in the North America and Scandinavia, *Larix* and *Pinus* are dominant in the forests of Siberia. Siberian larch (*Larix* sp.) forests cover some 278 million ha, or 64% of Siberia's total forested area (Osawa et al., 2010; Shvidenko and Nilsson, 1994). Scots pine (*Pinus sylvestris*) forests cover roughly 73 million ha, representing

Abbreviations: *a*, *b*, *c*, *f*, *g*, parameters; c_p , specific heat of air [J m^{-3}]; *VPD*, vapor pressure deficit [Pa]; *d*, zero plane displacement [m]; *DBH*, tree breast height diameter [cm]; *DOY*, day of year [ordinal day number]; E_c , stand (canopy) transpiration [mm]; ET_0 , reference evapotranspiration [mm]; g_a , aerodynamic conductance [m s^{-1}]; g_c , canopy conductance [m s^{-1}]; g_{\max} , maximal canopy conductance [m s^{-1}]; g_{\min} , minimal canopy conductance [m s^{-1}]; *PAR*, photosynthetically active radiation [$\mu\text{mol m}^{-2} \text{s}^{-1}$]; *Q*, tree sap flow [kg tree^{-1}]; R_0 , half light saturation [W m^{-2}]; R_g , global radiation [W m^{-2}]; R_n , net radiation [W m^{-2}]; T_a , air temperature [$^{\circ}\text{C}$]; $T_{a,\text{avg}}$, daily mean of air temperature [$^{\circ}\text{C}$]; *u*, wind speed [m s^{-1}]; w_s , volumetric soil water content in depth 10 cm [$\text{m}^3 \text{m}^{-3}$]; $w_{s,\min}$, minimal w_s in a growing season [$\text{m}^3 \text{m}^{-3}$]; γ , psychrometric constant [Pa K^{-1}]; Δ , slope of saturation water vapor pressure deficit [Pa K^{-1}]; λ , water heat capacity [J kg^{-1}]; ρ , density of dry air [kg m^{-3}]

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17% of the total area of forest area forest in Russia. Siberian larch (*Larix sibirica* Ledeb.) and Scots pine (*Pinus sylvestris* L.) occupy different ecological niches (Koropachinskiy and Vstovskaya, 2002). Larch typically grows at higher elevations in the mountains of southern Siberia and on permafrost primarily found in the north. Pine forests can be found at lower elevations in the mountains just south of the permafrost boundary and are more tolerant of waterlogged soils. Distribution patterns of the two species, however, are reportedly changing in response to climatic changes. This is also impacting potential interactions between each species and the environment (Shuman et al., 2011).

Climate models suggest that boreal forests will experience the largest degree of warming of any forest biome (IPCC, 2014). According to various global climate model predictions, Siberian boreal forests may experience temperature increases of between 3 °C and 5.5 °C by the end of the century. Increased drought occurrence and thawing permafrost will affect the water supply and, consequently, further shifts in the range of species distribution of larch and pine. The impacts of climate change and global warming have already been observed. The region of southern Siberia reported among the highest increases in drought severity (Dai et al., 2004). During the period 1991 to 2010, summer temperatures were reportedly 1–2 °C higher than those recorded from 1961 to 1990 (Tchepakova et al., 2011). Drier conditions and more regular water shortages in the south have favored Scots pine stands (Dulamsuren et al., 2009a), and weakened the overall vitality of Siberian larch growing in the same region (Dulamsuren et al., 2013). Pine stands have been observed to be moving to both higher latitudes and higher altitudes where they are effectively replacing larch stands (Kharuk et al., 2015, 2009, 2007). Shuman et al. (2011) predicted that Scots pine will eventually completely replace Siberian larch as the dominant tree species populating Siberian forests. Before that projected change in species composition is complete, larch forests will be forced to cope with unfavorable climate conditions.

The specific physiological responses of larch and pine to higher temperatures and drought conditions are likely to differ. Only a few studies have focused specifically on comparing ecophysiological traits of *Larix sibirica* and *Pinus sylvestris*. For example, based on a one-day measurement of photosynthesis and stomatal conductance, Dulamsuren et al. (2009b) reported that stomatal movements in *Pinus sylvestris* growing in northern Mongolia were more finely regulated in response to environmental factors than in *Larix sibirica*. More information is available in the literature on European larch, *Larix decidua*. The combined analysis of carbon isotopes and tree rings growth showed that *Larix decidua* is much more sensitive to drought than *Pinus sylvestris*, particularly those growing on xeric sites (Lévesque et al., 2013). As a deciduous conifer, larch must achieve high stomatal conductance during the summer months, irrespective of water deficits, to support the process of photosynthesis, while pine is photosynthetically active in the winter and early spring when evapotranspiration demands are relatively low (Lévesque et al., 2013). Anfodillo et al. (1998) and Leo et al. (2014) both reported high transpiration and assimilation rates for European larch when compared to Scots pine during periods with moderate water deficits. In a manipulative experiment designed to induce artificial drought, sap flow density was observed to decline by 63% in Scots pine, but only by 24% in European larch under the same drought conditions (Leo et al., 2014). Larch trees are able to maintain high transpiration rates by developing lower water potential than pine trees, which increases the risk of xylem cavitation and reduces tree vitality (Oberhuber et al., 2014). Viewed on a larger scale, increased transpiration of larch stands as a response to global warming combined with lower transpiration of pine forests which will have replaced larch stands may change the overall ecosystem-level water balance. As Kelliher et al. (1998) estimated by eddy covariance, as much as 90% of summer precipitation evaporated from the Siberian boreal forest into the atmosphere, while only 10% was absorbed by the groundwater. This shows us that even minute changes in transpiration may play an important role in mediating forest water balance. To our knowledge, no

comparative studies exist examining transpiration as a response to environmental drivers in larch and pine, two of Siberia's most important tree species.

In this study, we monitored canopy sap flow in two neighboring forest stands of *Pinus sylvestris* and *Larix sibirica* growing in the southern region of Central Siberia. Our experimental sites were located at the northern edge of the temperate forest zone, just south of the bordering boreal forests. We based our experimental on selecting trees that were the same age (49 years) in forest stands with similar ground basal area and similar leaf area index. This allowed us to compare both stand transpiration rates relative to environmental variables and determine absolute values of transpired water. We addressed the following questions: (i) what is the response of E_c and g_c on the atmospheric factors driving transpiration such as VPD , ET_0 , and R_g , (ii) how do the two different species respond to summer drought conditions and how important is soil water storage for E_c .

2. Material and methods

2.1. Study site and forest stands

Our study was performed at the Pogorelsky Bor research station of the Sukachev Institute of Forest SB RAS (56.36731 °N, 92.95543 °E, 247 m a.s.l.) near Krasnoyarsk, Russia. The mean annual T_a at the nearest meteorological station in the Sukhobuzimskoe village (56.49511 °N, 93.27905 °E) was 0.16 °C, while annual precipitation was 431 mm for the period 2006–2015 (RP5, 2017). Mean precipitation from April to September was 299 mm. *Larix sibirica* Ledeb. (Siberian larch) and *Pinus sylvestris* L. (Scots pine) were planted on two neighboring sites in 1970 as three-year-old seedlings; the age of the stand was 49 years at the time of our study conducted in 2016. No thinning or any other silvicultural treatments were performed during the stand development period apart from the removal of dead trees, which allowed the trees to form a closed canopy. The stem basal area of the larch stand was 59 m² and 58 m² for the pine stand. The average tree diameter at breast height was 17 cm and 25 cm and average height 21 m and 21 m for larch and pine, respectively. The leaf area index (LAI) was similar in stands of both species, 2.46 ± 0.17 in *L. sibirica* and 2.67 ± 0.12 in *P. sylvestris*. The soil was a sandy loam, grey podzolized, with several meters of sediment depth. The tree rooting depth was 1 m.

2.2. Meteorology and soil variables

Meteorological variables were measured approximately 100 m from the measured stands. The PAR, T_a , and air humidity were measured at a height of 2 m using a Minikin QTHi sensor (EMS Brno, Czech Republic) at 2-minute intervals. Wind speed was measured by a local weather station AMK-03 (IMCES, Russia) and precipitation by a Rain-O-Matic Professional rain gauge (Pronamic, Denmark). These data were used to calculate ET_0 (Allen et al., 1998). Soil water potential (between 0 and -1.5 MPa) and volumetric soil moisture were monitored in the larch stand at three depths (10, 20 and 45 cm) by three gypsum block sensors (GB2, Delmhorst Inc., USA) and with WaterScout SM100 sensors (Spectrum Technologies, USA), respectively. Soil temperature was measured in the same three depths by Pt100 thermometers. The sensors were connected to a data logger (RailBox V32P4E15, EMS Brno, Czech Republic), and an average of 10 min of data collected at 2-min intervals was stored in the memory.

The amount of water in the soil was calculated based on the mean value of soil water content obtained from three SM100 sensors and extrapolated to 1-meter depth. The length of each growing season was calculated based on the number of days with $T_{a,avg} > 5$ °C. The onset of a growing season was defined as the first of five consecutive days with $T_{a,avg} > 5$ °C and the end after five consecutive days of $T_{a,avg} < 5$ °C. Degree-day temperatures were calculated as the sum of positive differences between $T_{a,avg}$ and 5 °C from the beginning of the growing

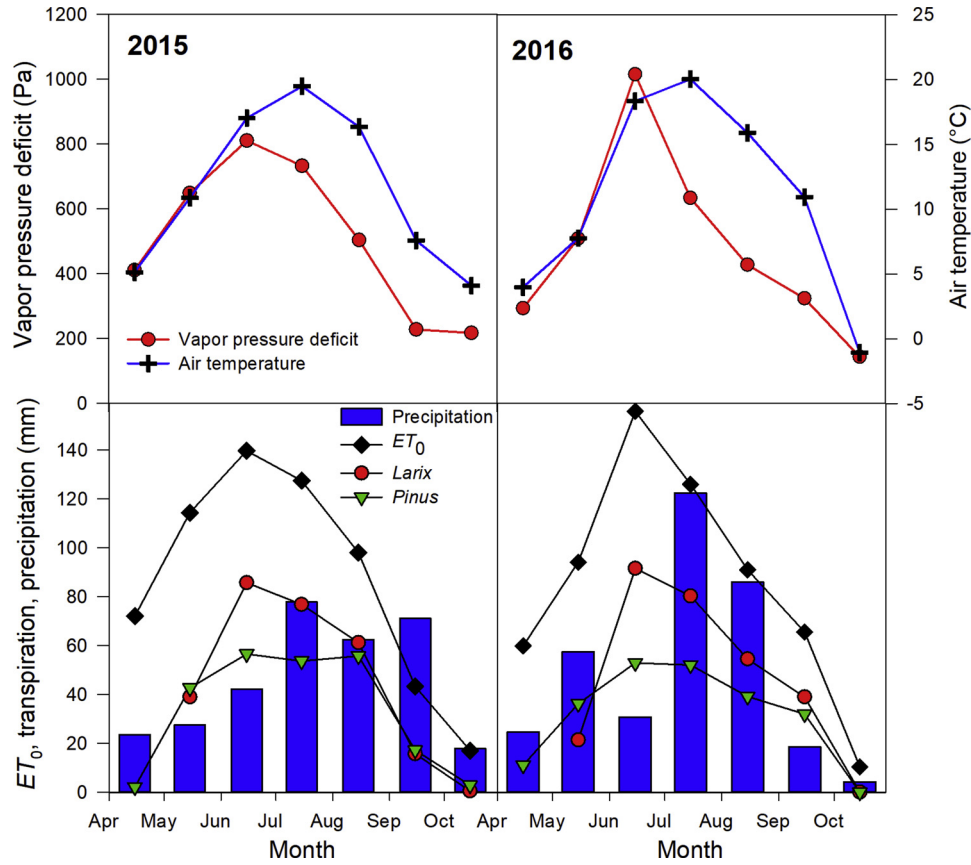


Fig. 1. Top: Monthly means of global radiation and air temperature from April to October in years 2015 (left) and 2016 (right). Bottom: Precipitation, grass reference evapotranspiration (ET_0) and transpiration of larch and pine canopy from April to October in 2015 (left) and 2016 (right).

season.

2.3. Sap flow

Six trees, from each species, considered representative of dominant, codominant and suppressed trees (diameters 15–26 cm in larch and 17–37 cm in pine) were selected for the sap flow measurements. We used the segment trunk heat balance (THB) method (Čermák et al., 2004, 1973). The sap flow sensors (EMS-51A, EMS Brno, Czech Republic) were installed at breast height, one on each tree, and covered with a reflective weather shield. The voltage outputs of the sensors were recorded by the data logger (Railbox V32, EMS Brno, Czech Republic) at 2-minute intervals, and 10-minute averages were stored in the memory. Sap flow was measured over the course of two entire growing seasons in 2015 and 2016. Scaling up of data from sap flow in the sample trees to the stand level was based on the DBH of the sample trees and diameter frequency distribution of the trees in each forest stand (Čermák et al., 2004). We used a scaling equation $Q = 933 \cdot DBH - 7749$ ($R^2 = 0.80$) to describe a relationship between the seasonal sum of Q and tree diameter of a larch tree, and the equation $Q = 0.294 \cdot DBH^{3.208}$ ($R^2 = 0.92$) to describe this same relationship in a pine tree.

The following equation was used to describe the dependence of sap flow on VPD:

$$E_c = a \cdot (1 - e^{(-b \cdot VPD)}) \quad (1)$$

And the equation

$$E_c = a + b \cdot (1 - e^{(-c \cdot ET_0)}) \cdot (1 - e^{(-f \cdot w_s)}) \quad (2)$$

was used to describe the dependence of sap flow on combined ET_0 and w_s . To parameterize these two equations, we used data with hourly

resolution and considered the period when the foliage had fully developed but had not yet become senescent (June 15 to September 15).

2.4. Derivation of canopy conductance

Canopy conductance was calculated using the Penman-Monteith equation (Kučera et al., 2017; Whitehead, 1998):

$$\frac{1}{g_c} = \left[\frac{\Delta}{\gamma} \left(\frac{R_n - \lambda E}{\lambda E} \right) - 1 \right] \frac{1}{g_a} + \frac{\rho c_p VPD}{\gamma \lambda E} \quad (3)$$

The variables listed above were directly measured or calculated (with the exception of soil heat flux). Zero plane displacement was set at $0.7 \cdot$ tree height and canopy roughness was $0.1 \cdot$ tree height. PAR was converted to R_g as $1 \text{ W m}^{-2} = 4.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Net radiation was calculated as 77% of R_g (Allen et al., 1998).

The analysis of the dependence of g_c on environmental variables was based on a version of the Jarvis Stewart model (Granier and Loustau, 1994):

$$g_c = a \cdot \frac{R_g}{R_g + R_0} \cdot \frac{1 - c \cdot VPD}{1 + f \cdot VPD} \cdot (1 - e^{-g_s \cdot (w_s - w_{s_{\min}})}) \quad (4)$$

Given that sap flow generally begins to move approximately one to four hours after transpiration occurs, we incorporated estimated time differences between R_g , VPD and sap flow by time cross-correlation analysis. This procedure was conducted individually for each tree species and separately for R_g and VPD. We only used lagged data for the parameterization based on the Jarvis-Stewart model.

2.5. Statistical analysis of data

Linear and non-linear regression analyses were done by minimizing

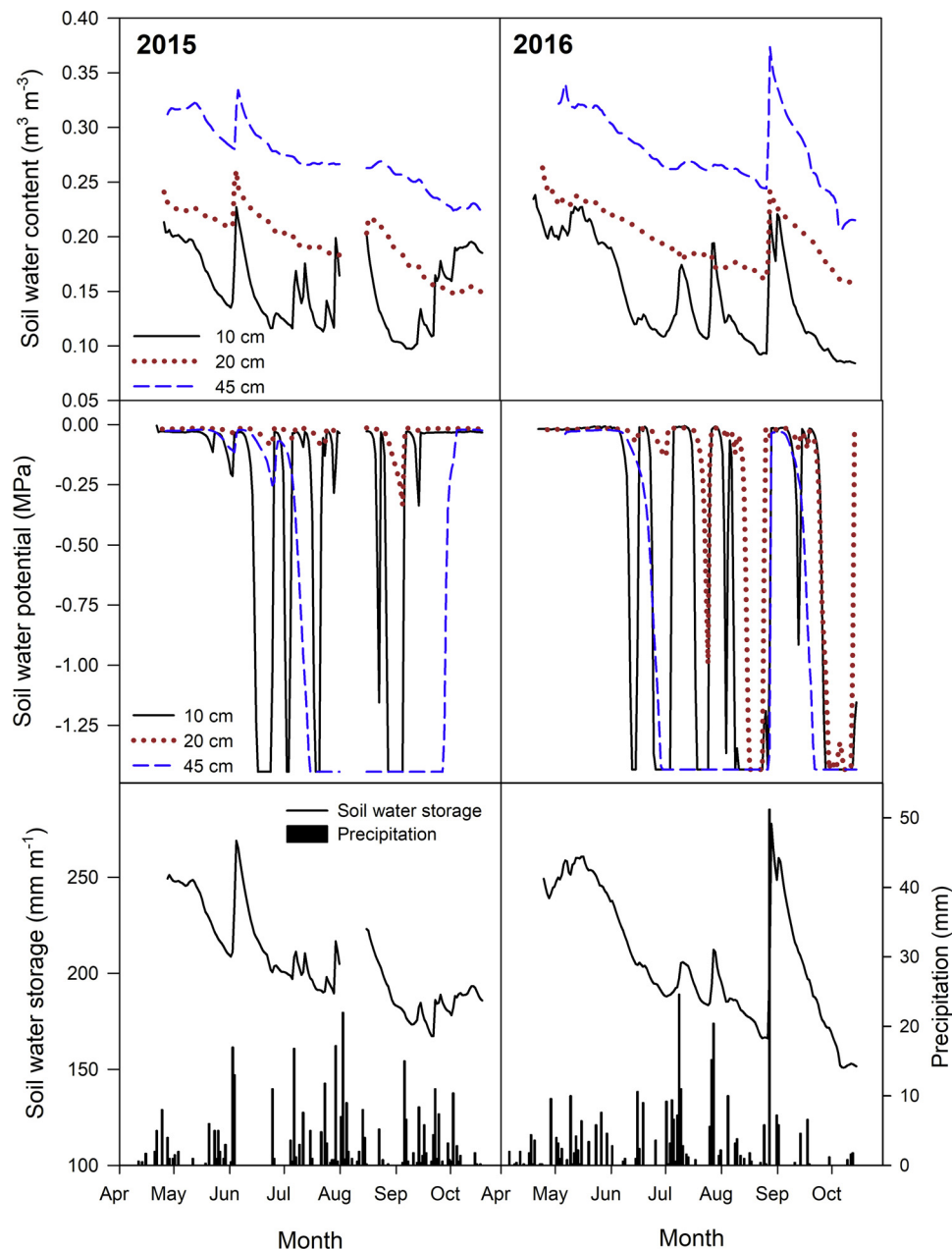


Fig. 2. Daily means of volumetric soil water content and soil water potential in three depths (10, 20 and 45 cm), the calculated amount of water stored in the top 1 m of soil and daily sums of precipitation from April to October in years 2015 (left) and 2016 (right).

the residual sum of squares. Curve and surface fitting to model 2D and 3D data was performed using Sigma Plot 12.5 software (SystatSoftware Inc., San Jose, CA, USA). To analyze differences between groups, analysis of covariance (ANCOVA) was used with *VPD* as a covariate, species as a factor and sap flow or g_c as the response variable. When the response variable did not depend on *VPD* we used analysis of variance (ANOVA) with a significance level 0.05. The R statistical program (R Core Team, 2015) was used for the statistical comparisons. Cross-correlation analysis was used to estimate time lag between sap flow, R_g , and *VPD*, which we performed using Mini32 software (EMS Brno, Czech Republic).

3. Results

3.1. Weather and soil water content

The research site described in this study was located in a region with

a continental climate characterized by cold winters, warm summers, and relatively low precipitation. The mean annual temperature was 2.9 °C and 1.0 °C, for 2015 and 2016, respectively (Table S1). The lowest temperature recorded in winter was −39 °C, while maximum summer temperatures reached 34 °C during this two-year period. The length of the growing season for 2015 was 157 days and 154 days in 2016. The mean temperature from April to September was 12.8 °C in 2015 and 14.6 °C in 2016 (Fig. 1, Table S1). The ET_0 reached 681 and 653 mm in 2015 and 2016, respectively, of which 593 and 532 mm were recorded from April to September. The sum of precipitation from April to September was 307 mm (2015) and 342 mm (2016) (Fig. 1). Precipitation was unevenly distributed with much higher levels recorded in summer months, and lower levels in the spring. The monthly sum of precipitation was almost always lower than ET_0 , which resulted in several spells of soil drought (Fig. 2). Soil water potential measured at a depth of 10 cm lowered over the course of the growing season to below −1 MPa at 26 days in 2015, and at 42 days in 2016. Given the

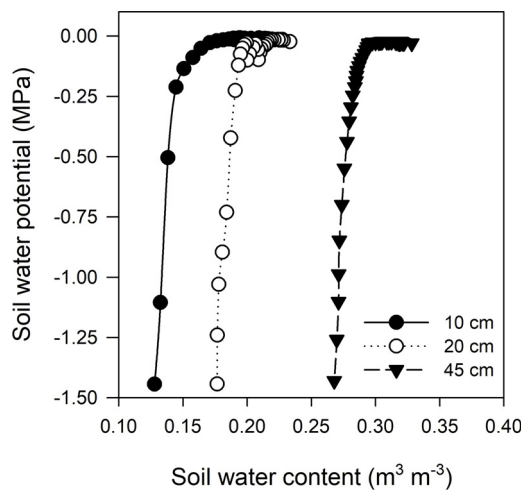


Fig. 3. The connection between soil water content and soil water potential in three depths, 10 cm, 20 cm and 45 cm.

increase in the percentage of clay particles consistent with soil depth, the water holding capacity and the relation between volumetric soil moisture and soil water potential also changed relative to soil depth (Fig. 3). The amount of water stored in the soil varied between over 250 mm m⁻¹ in the spring and about 150 mm m⁻¹ in the summer (Fig. 2).

3.2. Canopy transpiration

Overall, the larch stand transpired by 24% more water than the pine stand (Figs. 1 and 4). Accumulated E_c of the larch stand was 279 mm in 2015 and 287 mm in 2016, while the pine stand transpired 231 mm and 224 mm in the same years (Supplementary Table S1). Seasonal transpiration roughly accounted for 50% and 40% of the ET_0 in a single growing season for larch and pine, respectively. The E_c comprised between 67 and 91% of growing season precipitation, which was greater for larch than for the pine stand. Transpiration measured in June of both years, and additionally in May of 2015 and September of 2016,

was higher than precipitation levels during these months (Fig. 1), suggesting that some of the water stored in the soil (Fig. 2) was used for transpiration.

The diurnal sum of E_c reached up to 3.9 mm day⁻¹ in larch and 2.6 mm day⁻¹ in pine (Fig. 4). The two tree species differed in the distribution of E_c within the season. The first difference stemmed from their phenological type: larch is a deciduous conifer and pine is an evergreen conifer. The larch trees began transpiration later than pine, by 9 days in 2015 and by 26 days in 2016 (Fig. 4, Table S1). While transpiration for pine occurred just after the frozen soil melted at a depth of 10 cm, larch transpiration was initiated after bud break. Degree-day temperatures immediately preceding E_c for larch were 48 °C and 33 °C, which corresponded to soil temperatures 2.2 °C and 3.1 °C in 2015 and 2016, respectively. Threshold air temperatures just prior to E_c for pine were 29 °C in 2015 and 4 °C in 2016.

The second difference between the species occurred when the evapotranspiration demands were high. The difference between transpiration of larch and pine was the most pronounced in June (when ET_0 and VPD also peaked, Fig. 1) whereas transpiration for both species was almost equal from August through to the end of the season when atmospheric evapotranspiration demands were lower. Transpiration of larch peaked in June with 86 and 92 mm month⁻¹ and declined to 61 and 55 mm month⁻¹ in August 2015 and 2016, respectively. In contrast, transpiration of pine in June – August was stable and ranged between 52–57 mm month⁻¹, except for August 2016. When the VPD and ET_0 increased, sap flow in larch also increased, while sap flow rates observed in the pine leveled off (Figs. 5 and 6). Soil water content affected E_c in both species, however, E_c measured in the larch stand at a given water content level was consistently higher. The combination of ET_0 and w_s accounted for 86% and 80% of the variability in E_c measured for the period June 15 to September 15 (Eq. (2), Fig. 5). While sap flow at the same VPD gradually declined from June to August in larch, it did not lower in pine (Fig. 6).

Both tree species used water stored in their tissues for transpiration. The time lag of 90 and 120 min occurred between the sap flow and global radiation, which was shorter in larch than in pine. No time lag was observed between sap flow and VPD.

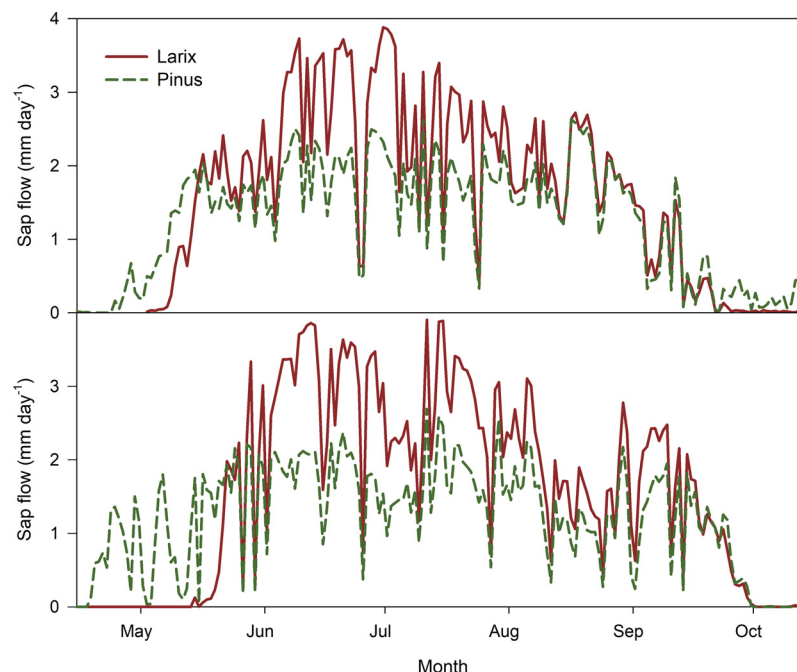


Fig. 4. Daily sums of sap flow of larch and pine canopies for 2015 (top) and 2016 (bottom).

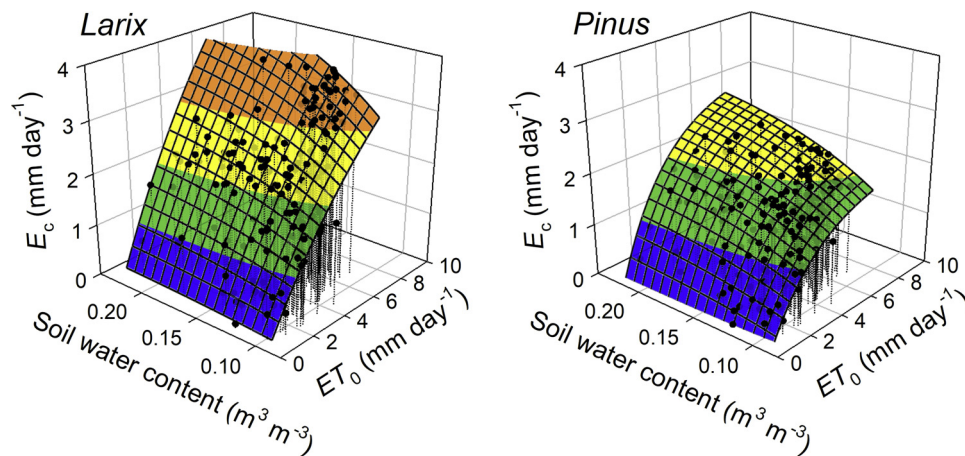


Fig. 5. The response of tree sap flow to changes in ET_0 and w_s in *Larix sibirica* (left) and *Pinus sylvestris* (right) from June 15 to September 15, in 2015 and 2016.

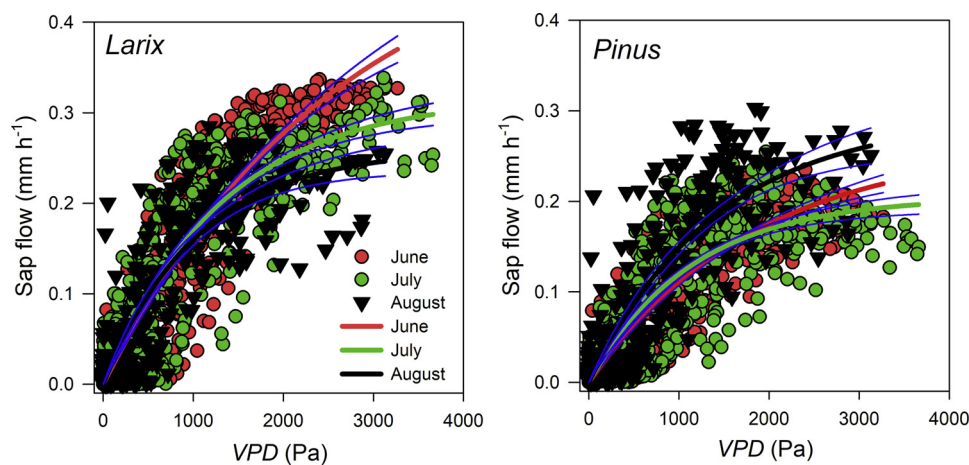


Fig. 6. Regressions between tree sap flow and VPD in *Larix sibirica* (left) and *Pinus sylvestris* (right), in June, July and August in 2015 and 2016.

3.3. Stomatal conductance

Stomatal conductance increased with R_g and declined with increasing VPD (Fig. 7). Larch g_c was higher than pine g_c ($p < 0.0001$). R_g , VPD, and w_s combined explained 66% and 42% of the variability in g_c observed in larch and pine, respectively, within the period June 15 to September 15 (Fig. 7, Eq. (4)). The g_c reached 50% of the maximum value when R_g was 68 and 188 $W m^{-2}$ in larch and pine, respectively. Both species closed their stomata in a response to growing VPD. Differences in g_c between the two species increased when VPD was high.

4. Discussion

The combination of low precipitation and high ET_0 resulted in high climatic water deficit of about 200 mm (Fig. 1) and frequent occurrences of summer drought (Fig. 2). Both species reduced their transpiration when the soil was dry or reduced g_c when atmospheric evapotranspiration demands were high (Figs. 5 and 7). Larch, however, exhibited much weaker stomatal regulation of transpiration than pine. Therefore, despite the shorter period with a green canopy and later start of transpiration (pine began transpiration in April, and larch in May, Fig. 4) the larch stand's seasonal amount of transpired water was 20% more than for the pine stand. The most pronounced differences between the two species were observed during months with the highest evapotranspiration demand, which were June and July. A gradual decrease of larch (but not pine) transpiration at high VPD from the beginning to the end of summer indicated a possible decline in overall hydraulic conductance of larch during this period.

Maximum diurnal E_c of the pine and larch stands in Siberia (2.9 and 3.9 $mm day^{-1}$, respectively) were close to maximum levels recorded in a Swedish mixed pine – spruce forest (3.6 $mm day^{-1}$) (Cienciala et al., 1999). Our results show that both studied stands transpired on a seasonal basis higher amounts of water than the boreal forest in central Sweden. This was mainly due to higher accumulated ET_0 corresponding to the continental climate of Siberia compared to Sweden's oceanic climate. There are no available data from similar sites, but we can draw comparisons between our study site and more northern forests where trees typically transpire less water than those located in the south. Evapotranspiration recorded from a larch forest growing on permafrost in Yakutsk (62°15' N) showed annual variations between 169–220 $mm year^{-1}$ with daily maximums above the dry canopy reaching 2.3 $mm day^{-1}$. Precipitation levels for this site, however, were half of those recorded for our site (Iijima et al., 2014; Ohta et al., 2008). One investigation proposed that evaporation from a Siberian pine forest (61° N) may reach 265 mm per growing season (Kelliher et al., 1998). Maximum E_c under these reported conditions was recorded as 1.5 $mm day^{-1}$ (Zimmermann et al., 2000). The particularly low E_c in this specific case can be attributed to both colder climate conditions with less precipitation and to stand structure; northern forests are more sparsely populated by trees with low leaf area index (Arneeth et al., 1996; Kelliher et al., 1998) and basal areas at breast height several times smaller than the basal areas of the trees populating our study stands (Zimmermann et al., 2000). We should also consider the possibility that larch trees growing in the far north may exhibit very different behavior than what we observed in the present study, such as much stronger stomatal regulation of transpiration (Kropp et al., 2017). Finally, earlier

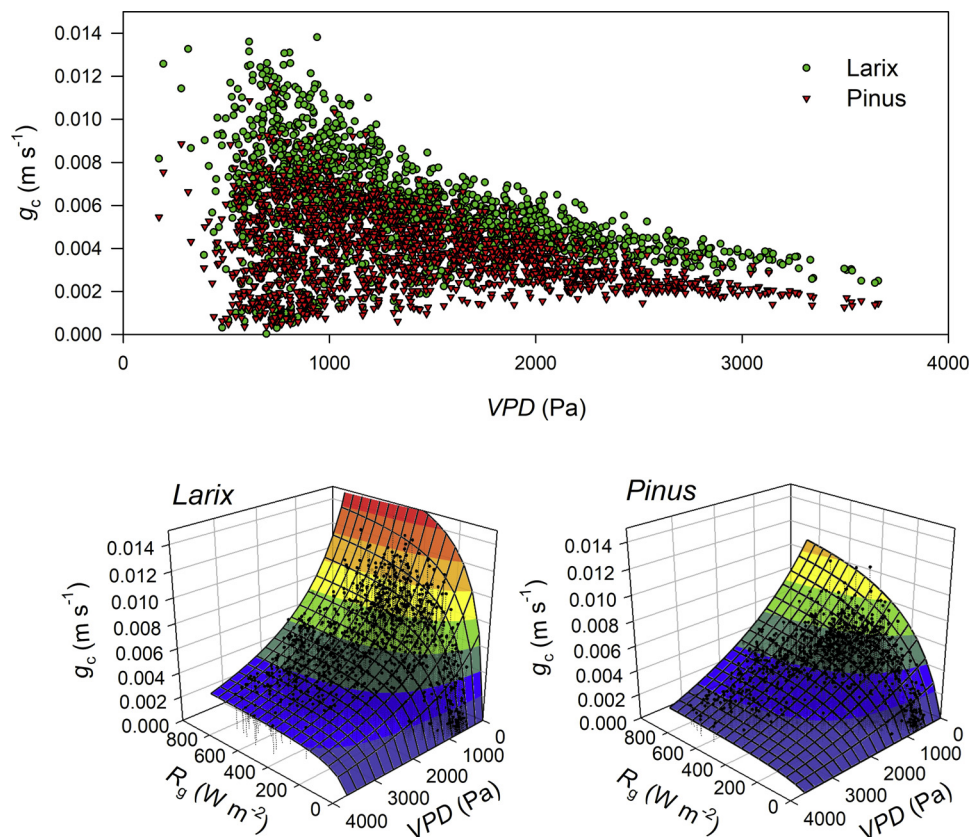


Fig. 7. The response of g_s to R_g and VPD in *Larix sibirica* (left) and *Pinus sylvestris* (right) from June 15 to September 15, in 2015 and 2016.

reports of low E_c values in Siberia may in part be explained by the method used for measuring sap flow. In these previous studies the authors used thermal dissipation sensors which, without proper calibration, can underestimate sap flow rate measurements by as much as 50% (Steppe et al., 2010), whereas in the present study we used a heat balance system.

Comparatively higher rates of transpiration observed in larch over pine in a context of high evaporative demands was previously described for European larch (*Larix decidua*) (Anfodillo et al., 1998). This dynamic was explained as the result of an adaptative strategy allowing larch trees to maintain high stomatal conductance and to regulate the amount of carbon assimilated throughout the seasons, essentially compensating for the fact that as evergreens, they bear green foliage for shorter periods. On the other hand, to maintain relatively high g_s in summer, the leaf water potential of larch would need to be relatively low. A comparative study of European larch and Scots pine in Austria suggested that minimum needle water potential of larch in summer under mild drought conditions was -3.0 MPa while in pine it measured only -1.8 MPa (Oberhuber et al., 2014). At our site and under mild drought (predawn water potentials -0.6 MPa and -0.5 MPa in larch and pine, respectively) on August 4, 2018, Siberian larch developed lower shoot water potential than Scots pine, too. Midday water potentials were -2.0 ± 0.18 MPa and -1.4 ± 0.19 MPa in larch and pine, respectively (Urban, unpublished). Even if conifers are, in general, relatively protected against cavitation (Choat et al., 2012), the difference in the degree of vulnerability to cavitation between larch and most other conifers is not significant (Charra-Vaskou et al., 2012). The fine roots with wide tracheids of the *Larix sibirica* make these trees particularly vulnerable to drought (Chenlemuge et al., 2015). Drought-induced cavitations and consecutive dieback of fine root biomass (Chenlemuge et al., 2013), therefore, may be the reason why larch E_c declined during the summer and why no decline was observed for E_c in the pine trees (Fig. 6). A previous study on stable isotopes in growth rings of five

European conifers indicated that larch and spruce were the most sensitive to drought, while pine was reportedly drought resistant (Lévesque et al., 2013). Notwithstanding the summer drought period, the lack of water in late spring which is a typical scenario for southern Siberia (the first drought spells occurred in June: Fig. 2) may have a detrimental effect on larch growth patterns. Drought is the likely the strongest contributing factor of tree top dieback frequently observed in larch trees populating Siberian forests in the northern regions and at the steppe boundaries in the south (Kharuk et al., 2007; O'Brien et al., 2017).

Changes in the global climatic conditions have progressed much faster than tree species are able to change their composition. It will take several hundred years before the transition takes place where larch forests are replaced by pine or mixed stands (Shuman et al., 2011). Before that happens, it is likely that we will see increased E_c in larch stands under increasingly warmer climate conditions. Our data collected from a "warm" site (where the mean temperature in July was 19 °C) with relatively high precipitation for Siberian boreal forests (over 400 mm year⁻¹), and from the forest with a closed canopy, may lead to a better understanding of high transpiration rates in Siberia under warmer climate conditions.

The water budget in the South Siberian forest steppe is already very tight given that this region is characterized by high potential evapotranspiration and low precipitation. Water stored in the soil has been an important source of water for driving transpiration in southern Siberia, as it was similarly reported for more northern forest sites growing on permafrost (Sugimoto et al., 2002). Currently, as much as 90% of summer precipitation in Siberian forests evaporates or is transpired back into the atmosphere (Kelliher et al., 1998). Therefore, we should expect that E_c will not increase linearly with increasing ET_0 , but rather the increase will be limited as a result of drought. On the other hand, transpiration observed in the Siberian larch, similar to European larch (Leo et al., 2014), was relatively less sensitive to the reduced

availability of soil water than Scots pine. Increasing E_c of forests will leave less water for the runoff. Our experimental site was in the watershed of Yenisey river. Summer and autumn discharge of this river has gradually declined by 15% over the last 50 years (presumably due to the higher evapotranspiration), even if the total discharge for this river during the entire year increased over those same 50 years (Shiklomanov et al., 2009). Lower water availability in forests will have negative impacts on plant diversity and will increase the frequency of forest fires (Brazhnik et al., 2017). The question remains how exactly the higher transpiration of larch stands in response to warmer climate conditions will be mitigated by a change in tree species composition towards more water-saving Scots pine forests.

5. Conclusions

Scots pine and Siberian larch differed in their environmental response of transpiration, especially under conditions of high atmospheric evaporative demand. Pine trees exerted stronger control over stomatal conductance which resulted in 20% less transpiration than larch trees under similar conditions. Transpiration rates for only larch trees gradually declined under conditions of high VPD from June to August indicating a decline in whole tree hydraulic conductance. Drought-related tree damage in boreal forests may be an important determinant of crown dieback in larch and their expected replacement by pine stands. In an increasingly warmer climate, low stomatal control of transpiration in larch will likely lead to increased evaporation from the boreal forests and more severe water deficits.

Declarations of interest

None.

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